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Assessing the effects of temperature and salinity oscillations on a key mesopredator fish from European coastal systems

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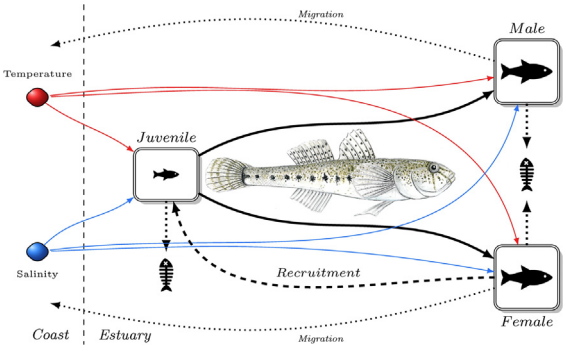
HIGHLIGHTS

- Extreme climatic events can be both beneficial or detrimental for *P. microps*.
- Simulations indicate that droughts can reduce the population of *P. microps*.
- *Simulations indicate that floods can benefit the population of P. microps.*
- Climate forecasts indicate that *P. microps* populations will shrink.

GRAPHICAL ABSTRACT



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ABSTRACT

A population dynamics model was developed to assess the short and long-term effects of temperature and salinity variations in the common goby *Pomatoschistus microps* in a Portuguese estuary (Minho estuary, NW Portugal). The population was divided into juveniles, females and males, which constituted the model's state variables. Linear regressions between the observed and the predicted density of juveniles, females and the total population were significant. Parameter's sensitivity and uncertainty analysis were estimated. The model was able to satisfactory describe the *P. microps* population dynamics, and thus was used to simulate the effects of climatic changes on the fish population. Simulations indicated that the common goby population is sensitive to both temperature and salinity changes. Overall, scenarios of more than 3 °C increase caused significant population decreases. Similarly, increased salinities led to a population shrinkage, whereas scenarios of salinity decrease generated an opposite variation on the population. According to the IPCC predictions for climatic tendencies, the population of the common goby will tend to decrease in the near future, experiencing marked oscillations (decrease or increase) during climatic extremes, namely droughts and floods, respectively. These results may be a useful for future planning and management of estuarine systems given that the common goby is an important species of estuarine food webs in many temperate ecosystems.

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1. Introduction

Estuaries are among the most complex, productive and valuable ecosystems (Costanza et al., 1997; McLusky and Elliot, 2004). A considerable number of aquatic species depend on these systems during different periods of their life cycle. Some species are residents and remain inside the estuary during their entire life cycle (Elliott et al., 2007), while others are migratory or transitory and use the estuarine area during shorter periods of time on their way to spawning grounds, where reproduction and/or juveniles' recruitment take place (Claridge et al., 1986; Potter et al., 1997). Furthermore, several other species use estuaries as nursery grounds (Beck et al., 2001; Peterson, 2003), given that they provide abundant prey resources and low predation risk for juveniles (Joseph, 1973), and sexually immature individuals can safely increase their feeding and growth rates (Houde, 1989; Cabral et al., 2007; Martinho et al., 2007).

Climate change is currently one of the most significant threats to biodiversity, it can affecting species phenology, metabolic costs, range of suitable areas of occurrence and ecological interactions among species, which can result in modifications on the structure, composition and dynamics of biological communities (Parmesan, 2006). The IPCC projections suggest that water temperature and salinity regimes will shift in coastal and transitional waters (IPCC, 2014). These changes are already occurring and influencing all trophic levels, from phytoplankton to carnivorous fishes (Beaugrand, 2009). However, up to date most studies on the effects of climate change on fishes have focused on commercially exploited species (e.g. Hare et al., 2010; MacKenzie et al., 2012). In contrast, studies that focus on small-sized fishes with no commercial interest are still scant. These species have an essential role in the structure and dynamics of food webs because they provide a link between species on lower and higher trophic levels (Doornbos, 1984; Moreira et al., 1992; Cabral, 2000). Their intermediate trophic position within food webs creates a "wasp-waist" flow control that can be amplified in systems harboring these species in very high densities (Coll and Libralato, 2012; Cury et al., 2000). In a global climate scenario it is expected that temperature and salinity will change in the near future (IPCC, 2014), and for this reason it is important to understand how changes in these two parameters will affect small-sized fish populations that occupy intermediate positions within trophic food webs.

The common goby (*Pomatoschistus microps*) is a very abundant and widespread small-sized fish occurring in temperate estuaries. This species is highly tolerant to environmental constraints, being able to tolerate a wide range of temperature and salinity, and thrive in harsh environmental conditions (Fonds, 1973; Moreira et al., 1992; Rigal et al., 2008). Despite this, several biological and ecological traits of *P. microps*, such as growth, reproduction, migration and mortality are highly dependent on the conditions of these two parameters (Jones and Miller, 1966; Fonds, 1973; Claridge et al., 1985; Wiederholm, 1987; Moreira et al., 1992; Rigal et al., 2008). The broad tolerance to temperature and salinity oscillations makes the common goby a good model species to assess the responses of biota to environmental changes, given that *P. microps* is theoretically less sensitive to minor changes on these parameters, and hence the shifts in its population dynamics can provide clear signs of responses to changes in environmental conditions.

Towards this end, a modeling approach was implemented to test the response of the small-sized fish species (*P. microps)* under different climatic scenarios. To preclude the possible effects of climate change in the common goby population, a system where the species is highly dense and productive was chosen (Souza et al., 2014). This study aims at understanding how a small-sized fish species that occupy intermediate positions within trophic food webs will be able to cope with changes on the climatic conditions.

2. Material and methods

2.1. Study area

This study was conducted in Minho estuary (NW Iberian Peninsula – 41°53′N 8°50′0W), which ranges up to 40 km (considering the upstream limit of spring tides), covering a total area of 23 km^2. This estuary is a shallow system (Moreno et al., 2005), with a mean depth of 2.6 m and maximum width of 2 km (Sousa et al., 2005; Freitas et al., 2009), and is characterized as a mesotidal and partially mixed system, although it tends towards a salt wedge estuary during periods of high river flow (Sousa et al., 2005).

The estuarine fauna is dominated by the European green crab (*Carcinus maenas*) and the common goby on the epibenthic compartment (Dias et al., 2010; Dolbeth et al., 2010; Souza et al., 2014; Mota et al., 2014), while two non-indigenous species (NIS), the Asian clam (*Corbicula fluminea*) and the red swamp crayfish (*Procambarus clarkii*), are the dominant macroinvertebrates in the study area (Sousa et al., 2008a, 2013). In fact, Minho estuary has been invaded by several aquatic NIS in the last decades, which impacted the system in various ways (Sousa et al., 2008b, 2013; Mota et al., 2014; Novais et al., 2015, 2016; Ilarri et al., 2015a, 2018).

Samples were collected at three sampling stations (S1, S2 and S3) located within the first 8 km of the Minho estuary, considering a gradient of distance to the river mouth (Fig. 1). S1 is located closer to the river mouth (ca. 1.5 km), and characterized by soft bottoms, often densely covered by debris (Souza et al., 2011, 2013, 2014, 2015). S2 is located within a salt marsh area (ca. 3.5 km upwards from the river mouth), with narrow channels, bordered by the small cordgrass *Spartina maritima*. The channels' soft bottoms are sparsely covered by debris and empty peppery furrow shells *Scrobicularia plana* (Souza et al., 2011, 2013, 2014, 2015). S3 is ca. 5 km upstream from S2, and is characterized by high densities of *C. fluminea*, with the soft bottoms also sparsely covered by debris and underwater vegetation (Sousa et al., 2008a, 2008c; Souza et al., 2013). Over the 12 months of the study the salinity and temperature at the three sampling stations ranged between 0.12 to 35.41 psu and 8.86 to 16.54 °C in S1, between 0.04 to 33.86 psu and 9.73 to 17.34 °C in S2, and between 0.03 to 27.51 psu and 8.31 to 20.46 °C in S3.

3. Data set

3.1. Fish and abiotic data

The model was developed and calibrated with data of *P. microps* sampled monthly, from February 2009 to January 2010. In each site, three replicates per month were collected using a 1 m beam trawl (5 mm mesh size) towed at constant speed (2 $km \cdot h^{-1}$) for two to three minutes, during daylight at high tide of spring tides (for further details see Souza et al., 2014, 2015). This sampling procedure has been shown to be equivalent to an average area of 100 ± 4 m^2 (Freitas et al., 2009). The density of *P. microps* was determined by counting all sampled individuals, and its density was then standardized to the same scale ($ind \cdot 100\ m^{-2}$). Density values input into the model refers to the average of the three sampling station per month, and the standard deviation was used as the confidence interval for model fit validation. Fifty randomly selected individuals from each sample were observed under a magnifying glass for sex distinction based upon dimorphic features on their morphology and gonads (Whitehead et al., 1986). Individuals smaller than 26 mm of total length showed no clear morphological signs of their sex, and were considered sexually immature and classified as juveniles (see Bouchereau et al., 1989). Females in advanced stage of development were considered mature and this information was posteriorly used to estimate the relative amount of mature females in the population. The total density of juveniles, males

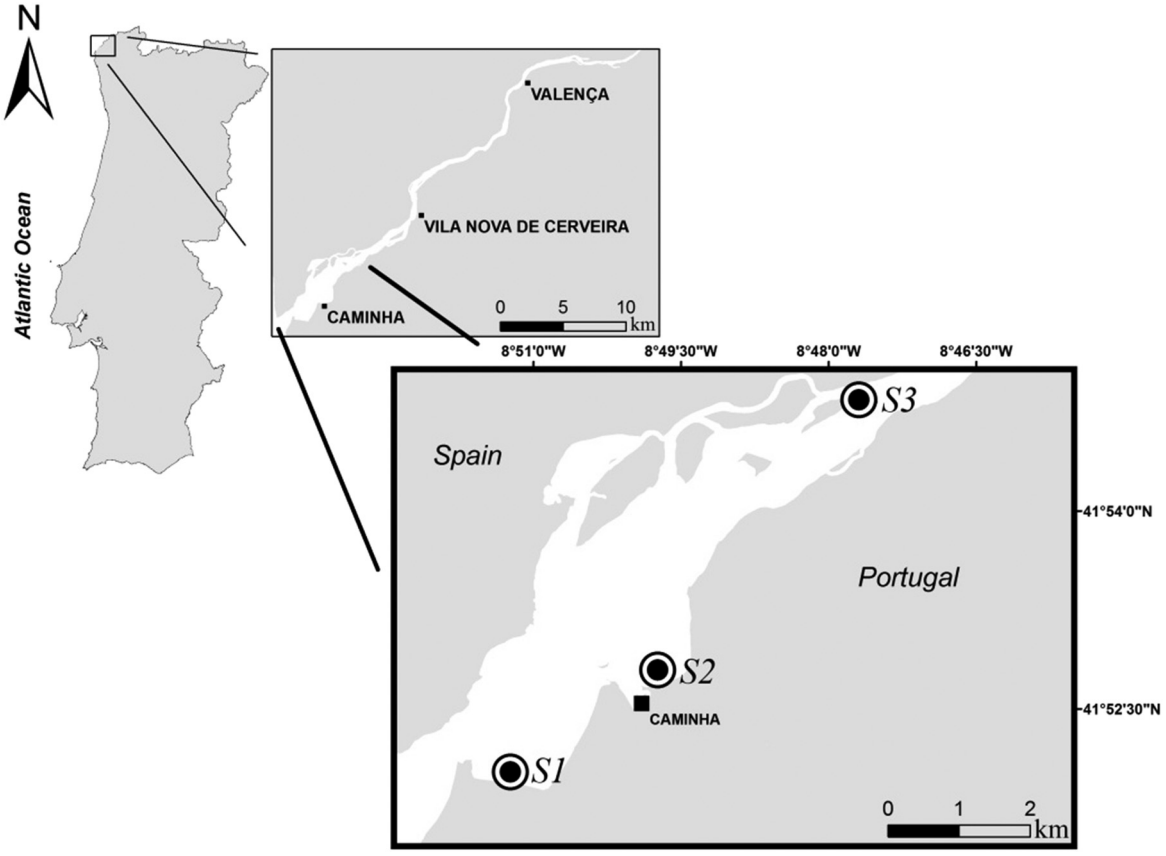

Fig. 1. Map of the study site showing the three sampling stations (S1, S2 and S3) at the Minho estuary, NW Iberian Peninsula.

and females was estimated based on the percentage of contribution of each group within the fifty randomly selected fishes from each sample.

The water temperature and salinity at the bottom were measured each month in the three sampling stations using a multiparameter probe YSI 6820.

The daylight duration data were obtained from NOAA website (http://www.esrl.noaa.gov/gmd/grad/solcalc/sunrise.html). Monthly daylight duration (minutes) was used as a proxy for the variation in day length at the study site.

4. Conceptualization and formulation of the model based on *P. microps* biological and ecological traits

Stage structured models have been proven to be advantageous because they account for different kinetics and parameters that regulate the dynamics and physiology of different life stages or groups of a given species (e.g. juveniles, males and females) (Batchelder and Miller, 1989; Labat, 1991).

In the present model, the estuarine *P. microps* population was divided into three groups: juveniles, females and males, which are the state variables of the model. The flows between state variables are individuals per unit of time, while the units of the state variables are individuals per 100 m^{-2}. The processes that regulate the number of individuals in each group over time are: growth, (the number of individuals transferred from one group to the next), death (the number of individuals subtracted to each group by mortality), migration (the number of individuals subtracted to females and males by the overwintering migration (Jones and Miller, 1966)), and recruitment (the input of juveniles to the population).

The model forcing functions were daylight duration, salinity and water temperature, which affect recruitment, growth, mortality and migration. The model was written in STELLA (Structural Thinking, Experimental Learning Laboratory with Animation) 5.0 software, an object-oriented graphical programming language designed specifically for modeling dynamic systems (Jørgensen and Bendoricchio, 2001), which translates the graphical representation of the model into ordinary differential equations (ODE). The model used a time step (i.e. temporal resolution) of one month to 12 (basic run) or to 240 months (projection simulations), that was chosen to allow a direct comparison with the data obtained in the field (Souza et al., 2014). A simplified conceptual diagram of the model is shown in Fig. 2. The parameters and equations that regulate the number of individuals in each population group are presented in Tables 1 and 2, respectively, and together with Fig. 2 outline the graphical and the mathematical description of the model. The justification of the values used in the model are explained in the following sub-sections.

Calibration refers to the systematic adjustment of model parameter estimates so that the model outputs reflect more accurately the observed dynamic behavior of the system. This procedure is applied when the available information for the parameters is likely to deviate from the normal behavior of the dynamic model. Calibration is a modeling tool often applied when the data for the parameter is adapted from a different system, the population displays heterogeneity and/or is subject to change through time (Beaudouin et al., 2008).

4.1. Sensitivity and uncertainty analysis

The sensitivity analysis of the model was estimated for variations of ±10% on each parameter at a time (i.e. all the other parameters were kept unchanged according to the one-step-at-a-time (OAT) approach). This method explores the parameter space and provides a robust sensitivity measure in the presence of nonlinearity and interactions among the parameters (Wainwright et al., 2014), being widely used in ordinary differential equations models (ODE) due to its simplicity and efficiency.

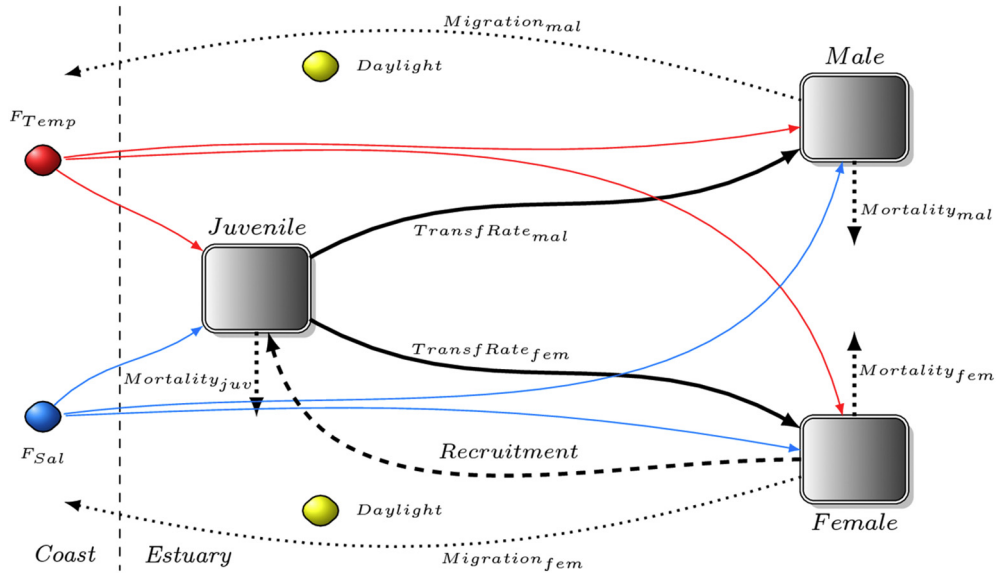

Fig. 2. Simplified conceptual diagram of the population dynamics model of the common goby *Pomatoschistus microps*. State variables are represented by shaded boxes, while the arrows represents the fluxes and interactions between parameters and state variables. All state variables and fluxes indicate the number of individuals in $100 \cdot m^{-2}$ per month.

To estimate the sensitivity of parameters, the following expression (Jørgensen, 1994) was used:

$$Y'_{Xi} = \frac{\partial Y}{\partial Xi} \quad (1)$$

where Y' is the sensitivity of the model outputs to variations on parameters (X_i).

The output of any model can be affected by different sources of uncertainty, including input data, choice of parameters, or calibration method, and thus it is important to have an explicit measure quantification of how much uncertainty affects models outputs (Confalonieri et al., 2016; Roux et al., 2014). To understand how much the model outputs could have been affected by the uncertainty in the measurements of the state variables we performed an uncertainty analysis (UA), on the four model parameters scoring highest in the sensitivity analysis (Table 3). These parameters are those most likely to affect the results

Table 1
Elements of the model and their respective values, symbols, description, units and estimation method, and initial values used on the model, when applied.

Type	Symbol	Description	Units	Used value
Equation	F_{sal}	Equation for the variation on salinity	Non-dimensional	Variable
Equation	F_{temp}	Equation for the variation on temperature	°C	Variable
Equation	$Migra_{fem}$	Number of migrating females	Per month	Variable
Equation	$Migra_{mal}$	Number of migrating males	Per month	Variable
Equation	$Mort_{fem}$	Mortality rate of females	Per month	Variable
Equation	$Mort_{juv}$	Mortality rate of juveniles	Per month	Variable
Equation	$Mort_{mal}$	Mortality rate of males	Per month	Variable
Equation	Recruitment	Number of juveniles entering in the system	Individuals·100 m^{-2}	Variable
Equation	Total abundance	Sum of the number of juveniles, females and males	Individuals·100 m^{-2}	Variable
Equation	$Transfer_{fem}$	Transfer rate from juveniles to females	Per month	Variable
Equation	$Transfer_{mal}$	Transfer rate from juveniles to males	Per month	Variable
Forcing function	Daylight	Monthly variation of the daylight duration	Minutes	Variable/experimental
Forcing function	Sal	Monthly variation of the salinity inside the estuary	Non-dimensional	Variable/experimental
Forcing function	Temp	Monthly variation of the water temperature inside the estuary	°C	Variable/experimental
Parameter	Egg loss	Rate of eggs not hatched in nests	Per month	0.30/literature
Parameter	Fecundity	Mean number of eggs generated per mature female	Per month	2000/literature; calibration
Parameter	Larval dispersal and mortality	Rate of larvae that fail to recruit	Per month	0.020338/literature; calibration
Parameter	Mature females	Rate of reproductive females	Per month	0.13/experimental
Parameter	$MigraRate_{fem}$	Rate of migrating females	Per month	0.65/calibration
Parameter	$MigraRate_{mal}$	Rate of migrating females	Per month	0.65/calibration
Parameter	$MortRate_{fem}$	Mortality rate of females	Per month	0.15/calibration
Parameter	$MortRate_{juv}$	Mortality rate of males	Per month	0.175/calibration
Parameter	$MortRate_{mal}$	Mortality rate of juveniles	Per month	0.20/calibration
Parameter	S_{max}	Maximum salinity for *P. microps* growth	Non-dimensional	51/literature
Parameter	S_{min}	Minimum salinity for *P. microps* growth	Non-dimensional	0.3/literature
Parameter	S_{opt}	Optimum salinity for *P. microps* growth	Non-dimensional	10/literature; calibration
Parameter	T_{max}	Maximum temperature for *P. microps* growth	°C	24/literature
Parameter	T_{min}	Minimum temperature for *P. microps* growth	°C	−1/literature
Parameter	T_{opt}	Optimum temperature for *P. microps* growth	°C	16/calibration
Parameter	$TransfRate_{fem}$	Rate of juveniles maturing into females	Individuals·100 m^{-2}	0.60/experimental
Parameter	$TransfRate_{mal}$	Rate of juveniles maturing into males	Individuals·100 m^{-2}	0.20/experimental
State variable	Female	Initial density of females	Individuals·100 m^{-2}	23/experimental
State variable	Juvenile	Initial density of juveniles	Individuals·100 m^{-2}	10/experimental
State variable	Male	Initial density of males	Individuals·100 m^{-2}	13/experimental

Table 2
Equations used in the model of the population dynamics of the common goby *Pomatoschistus microps* in Minho estuary, NW Iberian Peninsula. See Table 1 for abbreviations.

Juvenile density $Juvenile(t) = Juvenile(t\text{-}\partial t) + (Recruitment - Transfer_{mal} - Transfer_{fem} - Mort_{juv}) * \partial t$ Inflows: ○ $Recruitment = IF(Temp > 15)AND(Temp < 20)THEN(Female * Mature\ females * Fecundity * Egg\ loss * Larval\ dispersal\ and\ mortality * F_{temp} * F_{sal})ELSE(0)$ Outflows: ○ $Transfer_{mal} = Juvenile * TransfRate_{mal} * F_{temp} * F_{sal}$ ○ $Transfer_{fem} = Juvenile * TransfRate_{fem} * F_{temp} * F_{sal}$ ○ $Mort_{juv} = Juvenile * MortRate_{juv} * F_{temp} * F_{sal}$	Variation in juvenile density per unit of time	(1)
Male density $Male(t) = Male(t\text{-}\partial t) + (Transfer_{mal} - Mort_{mal} - Migra_{mal}) * \partial t$ Inflows: ○ $Transfer_{mal} = Juvenile * TransfRate_{mal} * F_{temp} * F_{sal}$ Outflows: ○ $Mort_{mal} = IF\ (Temp < 10)\ THEN\ (Male * MortRate_{mal} * 1.3)\ ELSE\ (Male * MortRate_{mal})$ ○ $MigraMal = IF(Temp < 10)OR(Daylight < 575)THEN(Male * MigraRate_Mal)ELSE(0)$ ○ $Migra_{mal} = IF\ (Temp < 10)\ OR\ (Daylight < 575)\ THEN\ (Male * MigraRate_{mal})\ ELSE\ (0)$	Variation in male density per unit of time	(2)
Female density $Female(t) = Female(t\text{-}\partial t) + (Transfer_{fem} - Mort_{fem} - Migra_{fem}) * \partial t$ Inflows: ○ $Transfer_{fem} = Juvenile * TransfRate_{fem} * F_{temp} * F_{sal}$ Outflows: ○ $Mort_{fem} = IF\ (Temp < 10)\ THEN\ (Female * MortRate_{fem} * 1.3)\ ELSE\ (Female * MortRate_{fem})$ ○ $Migra_{fem} = IF\ (Temp < 10)\ OR\ (Daylight < 575)\ THEN\ (Female * MigraRate_{fem})\ ELSE\ (0)$	Variation in female density per unit of time	(3)
Temperature $F_{temp} = IF\ (Temperature \le T_{opt})\ THEN\ (EXP(-2.3 * ((Temperature - T_{opt}) / (T_{min}\text{-}T_{opt}))^2))\ ELSE\ (EXP(-2.3 * ((Temperature - T_{opt}) / (T_{max} - T_{opt}))^2))$	Equation for the limit factor of temperature	(4)
Salinity $F_{sal} = IF\ (Salinity \le S_{opt})\ THEN\ (EXP(-2.3 * ((Salinity - S_{opt}) / (S_{min} - S_{opt}))^2))\ ELSE\ (EXP(-2.3 * ((Salinity - S_{Opt}) / (S_{max} - S_{opt}))^2))$	Equation for the limit factor of temperature	(5)

Table 3
Sensitivity (sensu Jørgensen, 1994) of the population density to ±10% variations of the parameters used on the population dynamics model of the common goby *Pomatoschistus microps* in Minho estuary, NW Iberian Peninsula.

Parameter	−10%	Base	+10%	Sensitivity
Egg loss	0.27	0.30	0.33	1.33
Fecundity	1800	2000	2200	1.33
Larval dispersal and mortality	0.0183042	0.020338	0.0223718	1.33
Mature females	0.117	0.13	0.143	1.33
$MigraRate_{fem}$	0.585	0.65	0.715	0.00
$MigraRate_{mal}$	0.585	0.65	0.715	0.00
$MortRate_{fem}$	0.135	0.15	0.165	−0.76
$MortRate_{juv}$	0.18	0.20	0.22	−0.27
$MortRate_{mal}$	0.135	0.15	0.165	−0.07
S_{max}	45.9	51	56.1	1.03
S_{min}	0.27	0.30	0.33	0.00
S_{opt}	9	10	11	0.34
T_{max}	21.6	24	26.4	0.15
T_{min}	−0.9	−1	−1.1	0.00
T_{opt}	14.4	16	17.6	0.48
$TransfRate_{fem}$	0.54	0.60	0.66	0.48
$TransfRate_{mal}$	0.18	0.20	0.22	−0.08

of the model, and thus we assessed the accuracy of the model by estimating its relative root square mean error (RRMSE) (Confalonieri et al., 2016). The lower the value of RRMSE, the lower the influence of uncertainty on the outputs of the model and higher is its accuracy. The UA allows to quantify the propagation of uncertainty in the model output that could be caused by natural variation and potential errors associated with the measurement of the state variables (i.e. the density of individuals in each group of the *P. microps* population) used in the model calibration. To this end, we used a Latin hypercube sampling (LHS) strategy (McKay et al., 1979) to generate a series of virtual observations for each state variable, and assuming a Poisson distribution. The LHS expands the concept of a Latin square for any number of dimensions. The distribution of each variable is divided in equally probable "n" number of intervals (strata). For each variable a sample is randomly drawn at each interval (McKay et al., 1979), and the values of each variable are then randomly paired to each other. This is a type of stratified random sampling procedure that can be understood as a compromise between a random and stratified sampling techniques that provides a stable analysis outcomes (Helton and Davis, 2003), and is not computationally demanding. The efficient stratification obtained with the LHS allows the use of a relatively low small sample (10n, with n being the number of observations in the empirical dataset) of the distribution space of the variables (Helton and Davis, 2003). Thus, we generated a virtual series of 90 observations for each state variable, which represents the data that could have been collected due to the uncertainty in the sampling procedure (Confalonieri et al., 2016). With each data series we recalibrated the most sensitive parameters in the model while accounting for the uncertainty in the measured state variables. The outputs obtained with the virtual data series were then used to estimate the objective function of the RRMSE between the observed data and the model output for each of the virtual series. The RRMSE function was minimized using a multi-start point downhill simplex optimization algorithm (Nelder and Mead, 1965). The distribution of the RRMSE values of the model outputs obtained by calibration with the virtual data series was compared against that of the model outputs obtained by calibration with the empirical data (Confalonieri et al., 2016).

The virtual data series was generated with function *randomLHS* from the package *lhs* (Carnell, 2018), the RRMSE calculated with function *rrmse* from the package *Fgmutils* (Fraga Filho et al., 2016), and the RRMSE minimization with function *optim* from the package *stats*, for R software (R Core Team, 2015).

4.2. Studied species

The common goby *Pomatoschistus microps* is a widely distributed estuarine species spanning ca. 44° in latitudinal range, occurring from Norway to Mauritania, including the Canary Islands, western Mediterranean and Baltic Sea (Froese and Pauly, 2016). This species is often reported as one of the most abundant fish in northern Atlantic estuaries (Martinho et al., 2007; Dolbeth et al., 2010). *P. microps* is frequently found in areas where the sympatric goby *P. minutus* co-occurs and both species tend to present similar densities (Arruda et al., 1993; Leitão et al., 2006; Martinho et al., 2007; Dolbeth et al., 2010). However, in Minho estuary the common goby seems to be much more abundant than the sand goby, presenting a remarkably dense and productive

population, which is attributed to site-specific favorable conditions (Souza et al., 2014, 2015).

4.2.1. Reproduction and recruitment

The reproductive behavior of *P. microps* is relatively well known, with spawning occurring usually when the water temperature ranges between 15 and 20 °C (Wiederholm, 1987). During the reproduction season, mature females lay eggs on nests built by males using empty bivalve shells (Nyman, 1953; Jones and Reynolds, 1999; Pampoulie, 2001). Males fertilize the eggs, fan and guard them until hatching (Svensson et al., 1998; Jones and Reynolds, 1999; Pampoulie, 2001). During nest guarding behavior, males often prey on their own brood (Magnhagen, 1992) removing ca. 30% of the egg mass of a clutch (Forsgren et al., 1996).

Common gobies are known to have a high individual fecundity (Bouchereau and Guelorget, 1998), with each mature female being able to generate from 460 to 3400 eggs (Miller, 1986; Bouchereau et al., 1989; Bouchereau and Guelorget, 1998), but the mortality rate during the early stages of fish development is also very high (Leis, 2007). In fact, the survival rate of marine and diadromous fish larvae varies between 6.7×10^{-5} and 0.1% (Dahlberg, 1979). No information was found in the literature regarding the mortality rate of *P. microps* larvae, and due to this, the value of larvae mortality used in the model was obtained through calibration and based on values of other marine and estuarine fishes.

The percentage of mature females on the population during spawning season was estimated as the ratio between the number of females in advanced stages of gonadal development and the total number of females.

The lag between spawning and recruitment was established in one-time-step, given that the species has a very short larval phase (2 to 10 days), and the recruitment likely occurs shortly after (Riley, 2003).

4.2.2. Mortality

One of the most important shortcomings in the knowledge of estuarine fishes is the lack of estimates on the source of mortality for any life history stage (Houde, 2008). Even where mortality estimates have been made for estuarine species, the influence of confounding factors (i.e. gear avoidance, inaccessible habitats, etc.) makes it difficult to determine mortality rates (Able and Fahay, 2010). As far as we know, there is no published paper addressing the mortality rate of the common goby in nature, therefore mortality rates used in the model were obtained through calibration. Given that juveniles, females and males of this species can behave differently, we assume that their mortality rate is also different (Magnhagen, 1992; Svensson et al., 1998).

Notwithstanding, mortality rate may vary throughout the year in temperate estuarine fishes (Able and Fahay, 2010). In fact, during winter, small and relatively immobile fish experience an increase in their mortality rates, due to net energy deficits caused by low temperatures and food scarcity (Sogard, 1997; Hurst et al., 2000; Hales and Able, 2001; Hurst, 2007). This may lead to an increase in the mortality of estuarine fish of about 33% during winter (Able and Fahay, 2010). The seasonal variation of *P. microps* mortality was taken into account in the model by assuming an increment of 30% in the mortality rate of all population groups when water temperature was below 10 °C.

The number of *P. microps* individuals subtracted to each population group was defined by:

$$Mortality_i = MortRate_i \times D_i \quad (2)$$

where $Mortality_i$ = mortality of the population group i; $MortRate_i$ = mortality rate of the population group i; D_i = density of the population group i.

The parameters values and the equations of each population groups are presented in Tables 1 and 2, respectively.

4.2.3. Migration

The typical life cycle of the common goby lasts for one year, with adults migrating to warmer waters during winter (Jones and Miller, 1966; Muus, 1967). Given that the common goby presents a dynamic and plastic behavior in several life traits (Reynolds and Jones, 1999; Pampoulie et al., 2000; Heubel et al., 2008), it is expected that the temperature level which triggers seasonal migration in estuarine populations should also be different across the geographical range of the species (Jones and Miller, 1966). For instance, Jones and Miller (1966) reported that migration is triggered when temperature is lower than 7 °C, while Claridge et al. (1985) mentioned that at 5 °C migration is triggered. For other estuarine overwintering migrating species in nearby systems, it is argued that 10 °C is responsible for triggering seasonal migration (Gomes, 1991). Given the scarcity of information regarding the temperature level that triggers overwintering migration of common gobies in Southern European estuaries, we have considered reasonable to assume that temperatures lower than 10 °C induce *P. microps* migration in Minho estuary.

Moreover, migration can also be triggered by other environmental cues, such as precipitation, drought, water discharge and photoperiod (Bauer et al., 2011). In a recent study, McNamara et al. (2011) suggested that photoperiod is probably the most prominent and universal variable, indicating that the time of the year can also be relevant to several organisms. Photoperiod is a reliable indicator of the time of the year, and thus, can be a useful predictor of the phenology of resources (Bauer et al., 2011). In this context, the photoperiod was also taken into account in the migration equation. The number of migrating *P. microps* individuals in each population group was defined by:

$$Migra_i = MigraRate_i \times D_i \quad (3)$$

where $Migra_i$ = migration of the population group i; $MigraRate_i$ = migration rate of the population group i; D_i = density of the population group i.

4.2.4. Effect of temperature and salinity on growth

Since *P. microps* is not able to control its body temperature to a significant degree, the typical response is that its metabolic rate varies directly with ambient temperature (von Oertzen, 1983). The common goby presents a relatively wide tolerance range for temperature variation, and is able to cope with temperatures ranging from −1 °C to 24 °C (Fonds, 1973; Moreira et al., 1992). Freitas et al. (2010) assumed that the optimal temperature for *P. microps* growth is 20 °C, but since this value could not be experimentally validated, the value used in the model was obtained by calibration, using the optimal temperature reported by Freitas et al. (2010) as a proxy.

Salinity is one of the most important environmental factors affecting the growth and survival of aquatic organisms, influencing both physiological and ecological processes (Poizat et al., 2004; Nordlie, 2006), and many studies have demonstrated the influence of external salinity on growth capacities of fishes (Bœuf and Payan, 2001). The metabolic rate of *P. microps* varies directly with salinity (Rigal et al., 2008), and the species has a relatively wide tolerance for salinity variation, withstanding salinities ranging from 0 to 51 psu (Rigal et al., 2008), though better physiological performances occur at low salinities (Pampoulie et al., 2000; Rigal et al., 2008). To cope with this, the model used an optimum curve to describe the effect of salinity on *P. microps* growth. The optimum salinity value for the species (SOpt) was obtained in the literature and then calibrated (see Table 1).

The effect of temperature and salinity on *P. microps* growth was described as an optimum-type curve (Martins et al., 2008), where:

$$f(i) = e^{-2.3}\left(\frac{(i - i_{opt})}{(i_{min} - i_{opt})}\right)^2 \text{ for } i \le i_{opt} \quad (4)$$

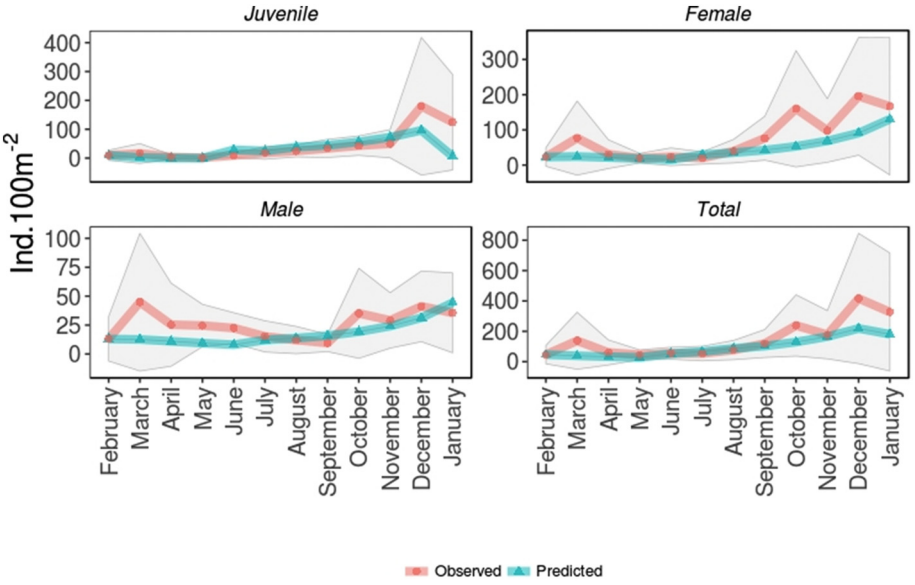

Fig. 3. Observed ± SD (shaded ribbon) and predicted variation of juveniles, females, males and the total density (ind·100 m^{-2}) of the common goby *Pomatoschistus microps* in the Minho estuary, NW Iberian Peninsula.

and

$$f(i) = e^{-2.3}\left(\frac{(i-i_{opt})}{(i_{max}-i_{opt})}\right)^2 \text{ for } i>i_{opt} \quad (5)$$

where i = temperature/salinity; i_{opt} = optimum temperature/salinity for growth; i_{min} = minimum temperature/salinity at which growth ceases; i_{max} = maximum temperature/salinity at which growth ceases.

Long run simulations (240 months) were performed to test the stability of the model.

4.3. IPCC predictions

The IPCC (Intergovernmental Panel on Climate Change) Fifth Assessment Report (AR5) predicted that surface air warming in the 21st century will range from 1.1 to 6.4 °C (IPCC, 2014). Also, the annual temperature over Europe will increase at a rate of 0.1 and 0.4 °C per decade, and warming will be greater in southern Europe and northeast Europe (IPCC, 2014).

The IPCC projections show that the annual precipitation will decrease across southern Europe (maximum 1% per decade), resulting in drier summers and wetter winters (IPCC, 2014). This is likely to cause changes on the salinity levels of estuarine systems, since droughts and floods events will be more frequently triggered in these systems, as recently reported (Cardoso et al., 2008; Dolbeth et al., 2010; Santos et al., 2010; Ilarri et al., 2011).

In this context, several scenarios of temperature and salinity variations in Minho estuary were simulated. Four levels of water temperature increasing (+1, +2, +3 and +4 °C) and four levels of salinity change (−5 psu, +5 psu, +10 psu, and oscillatory (−5 psu from November to April and +5 psu from May to October)) were simulated. Additionally, the combined effects of temperature and salinity variations were also simulated.

Finally, we performed projection simulations (for 20 years) to assess the extended effects of expected temperature and salinity variations in Southwestern Europe under different climatic change scenarios on the common goby population in Minho estuary. Two different rates of temperature increase were simulated: slow (+0.01 °C per year) and rapid (+0.04 °C per year), combined with different scenarios of salinity (normal, −5 psu, +5 psu, and oscillatory). The initial conditions of the simulations followed the conditions measured in the field accompanied by the modification related to the scenarios of temperature and salinity tested in each simulation.

5. Results

5.1. Model results

The density of *P. microps* juveniles predicted by the model followed the same pattern as the observed variation, with a marked peak of abundance in December (Fig. 3). The density predicted for females, males and total population also followed similar patterns than those of the observed data, with density continuously increasing after spring and reaching a peak in December or January (Fig. 3).

5.2. Model stability, sensitivity and uncertainty analysis

The model showed long-term stability, which supports the internal logic of the model (Jørgensen, 1994). The sensitivity analysis identified

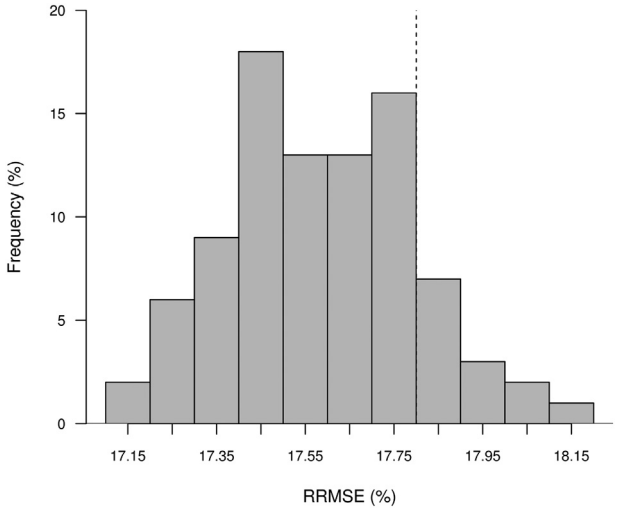

Fig. 4. Frequency distribution (%) of the relative root mean square error (RRMSE, %), obtained by recalibration of the most sensitive parameters in the model and using the virtual data series generated with the Latin hypercube sampling technique. Dashed vertical line refers to the RRMSE by calibration of the model with the empirical data.

Table 4
Linear regressions between the observed and the predicted values for the common goby *Pomatoschistus microps* density inside Minho estuary, NW Iberian Peninsula. SS = sum of squares, MS = mean square, F = F-statistic, SD = standard deviation (slope), * = statistically significant, ns = statistically non-significant.

Group	SS	MS	F	Slope	SD	R^2	P
Juvenile	11,559	11,559	5.50	1.04	0.44	0.35	<0.05*
Female	32,750	32,750	26.12	1.56	0.31	0.72	<0.001*
Male	349.4	349.4	2.95	0.53	0.31	0.23	0.12ns
Total	135,941	135,941	46.52	1.73	0.25	0.82	<0.001*

the parameters related to reproduction (egg loss, fecundity, larval dispersal and mortality, mature females) to be the most sensitive (Table 3). The uncertainty analysis carried out through the recalibration of the most sensitive parameters with the data series generated by the LHS delivered a very narrow frequency distribution of the RRMSE values, ranging from 17.10% and 18.20%. Most of these were lower than that obtained with the empirical data (17.82%, Fig. 4). However, the RRMSE value of the empirical model was still low thus well within the range obtained with the virtual data series (Fig. 4), indicating that uncertainty had low influence on the empirical model outputs.

5.3. Climatic change simulations

Once the correlation between the model outputs and real data was shown to be satisfactory (Table 4), the model was considered suitable to simulate the effects of the forthcoming climatic changes on the common goby population during a year cycle (12 months).

5.4. Temperature variations

Simulations suggest that *P. microps* population will be greatly affected by water temperature warming. For low increases of temperature scenarios, the overall density of *P. microps* would increase by 3%, 33% and 58% for (+1 °C, +2 °C and +3 °C, respectively) in the one year simulation, while in the +4 °C scenario the common goby population would decline on a year basis by 21% (Fig. 5). Also, the timing of the density peaks changed for the increasing water temperature scenarios, with the juveniles recruiting earlier in the year in all scenarios except in +1 °C. In +4 °C scenario, the density peak of juveniles will change from December to June, while females and males peaking in July instead of January (Fig. 5).

5.5. Salinity variations

Simulations accounting for salinity variations suggest that *P. microps* population would be benefited by a decrease in salinity (19% increase of the total density in one year), while an increase (+5 and + 10 psu) or an oscillatory pattern in salinity would lead to a decrease in *P. microps* population (25, 44% and 24%, respectively) (Fig. 6).

5.6. Combined effects of temperature and salinity variations

Overall, the combined effects of temperature and salinity increase would lead to a decrease in *P. microps* population in all scenarios, except the +3 °C combined with a decrease of 5 psu in salinity (19% increase). When oscillatory pattern in salinity is combined with temperature increase fish population would decline only in +1 °C and +4 °C (21% and 33%, respectively), while an increase of 8% and 19% would be observed for +2 °C and +3 °C scenarios, respectively. On the other hand, a temperature increase combined with a salinity decrease would cause a noticeable increase in population levels of *P. microps* for all scenarios (ranging from 23% to 61%), but it is in +4 °C that the population would decline by nearly 30% in a year cycle (Fig. 7).

5.7. Projection simulations

According to results, temperature increase for longer periods of time would have significant consequences for *P. microps* population in Minho estuary, with a continuous decrease in population density throughout time in all scenarios (Fig. 8). Similarly an oscillatory pattern of salinity or a salinity increase would lead to a marked decrease in *P. microps* population, while a salinity decrease would have the opposite effect (Fig. 9).

The combined effects of temperature increase and salinity variation will cause an even faster decrease of *P. microps* density levels in all scenarios accounting for an oscillatory salinity pattern or salinity increases. On contrary, with salinity decreases, the common goby population will initially decrease, recovering after 20 years on the slow IPCC scenario. Conversely, on the rapid IPCC scenario, the population would immediately increase, reaching density values 5 times higher than when compared to the present situation (Fig. 10).

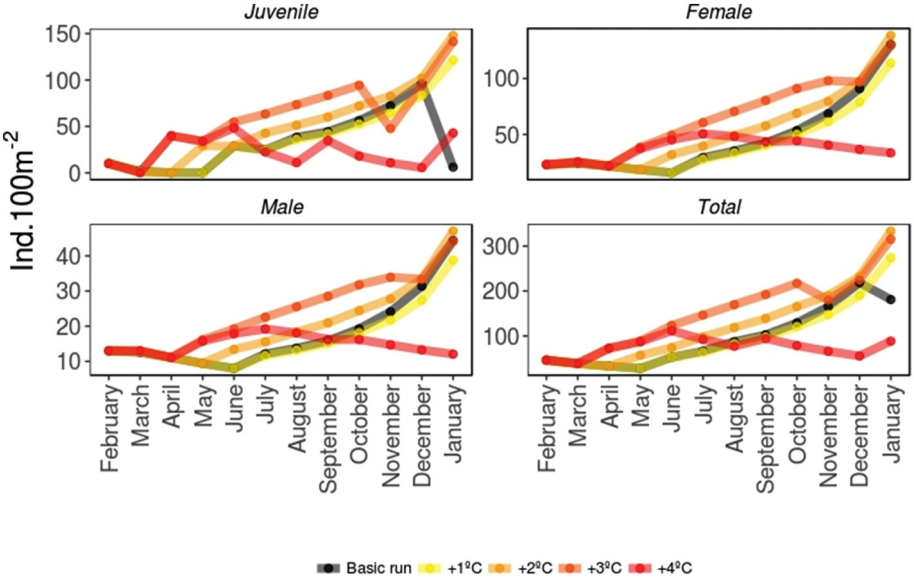

Fig. 5. One year simulations of juveniles, females, males and total density (ind·100 m^{-2}) of the common goby *Pomatoschistus microps* in different scenarios of temperature increase according to the IPCC projections (IPCC, 2014).

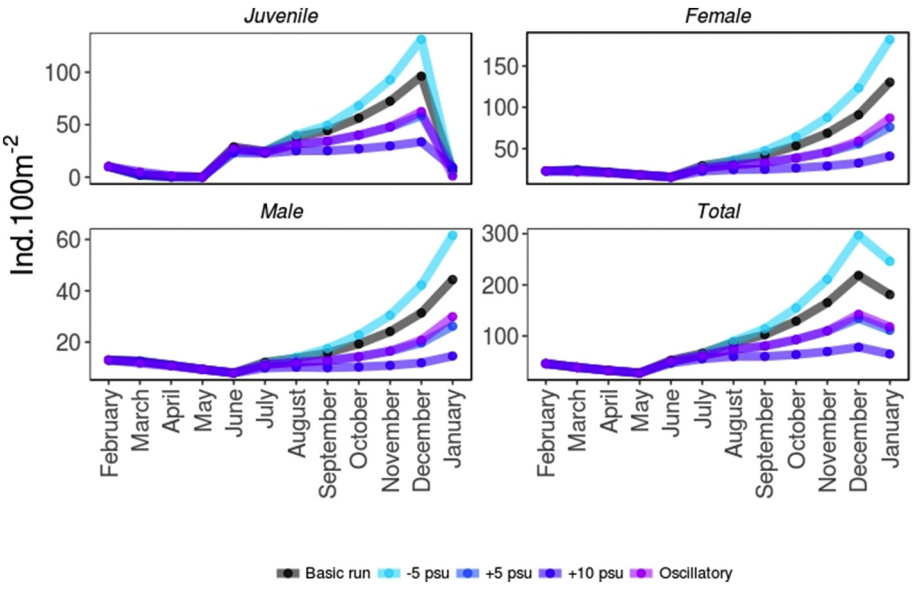

Fig. 6. One year simulations of juveniles, females, males and total density (ind·100 m^{-2}) of the common goby *Pomatoschistus microps* in different scenarios of salinity decreasing (−5 psu) and increasing (+5 psu, +10 psu) and oscillatory pattern (−5 psu from November to April, and +5 psu from May to October).

6. Discussion

The model was capable to satisfactory simulate the variation of *P. microps* density and dynamics at the Minho estuary. Projection simulations indicated that *P. microps* population will be highly sensitive to changes in both temperature and salinity. According to predictions, rises in water temperature will cause long-term detrimental effects on *P. microps* population, with harsher scenarios affecting *P. microps* more severely.

Furthermore, predictions also suggest that the spawning season might change due to increasing water temperature. In milder scenarios, changes in spawning season might be associated to an extension of the recruitment season, with common gobies spawning earlier in the year. However, in harsher scenarios, the spawning season will be greatly altered, with juveniles starting to recruit in winter but with a marked shortage in the duration of the recruitment season. According to experimental evidence, the duration of spawning seasons has a major effect on *P. microps* populations (Bouchereau and Guelorget, 1998), and it may be one of the reasons behind the high density of the species in Minho estuary, once in this system, the reproduction season appears to be longer than in other estuaries (Souza et al., 2014).

Freitas et al. (2010) assumed that the optimal temperature for *P. microps* growth is 20 °C. Nevertheless, previous empirical observations (Dolbeth et al., 2010) and the results from the present model indicated that the species is more abundant and productive at lower temperatures. However, unless specific experimental studies are conducted to

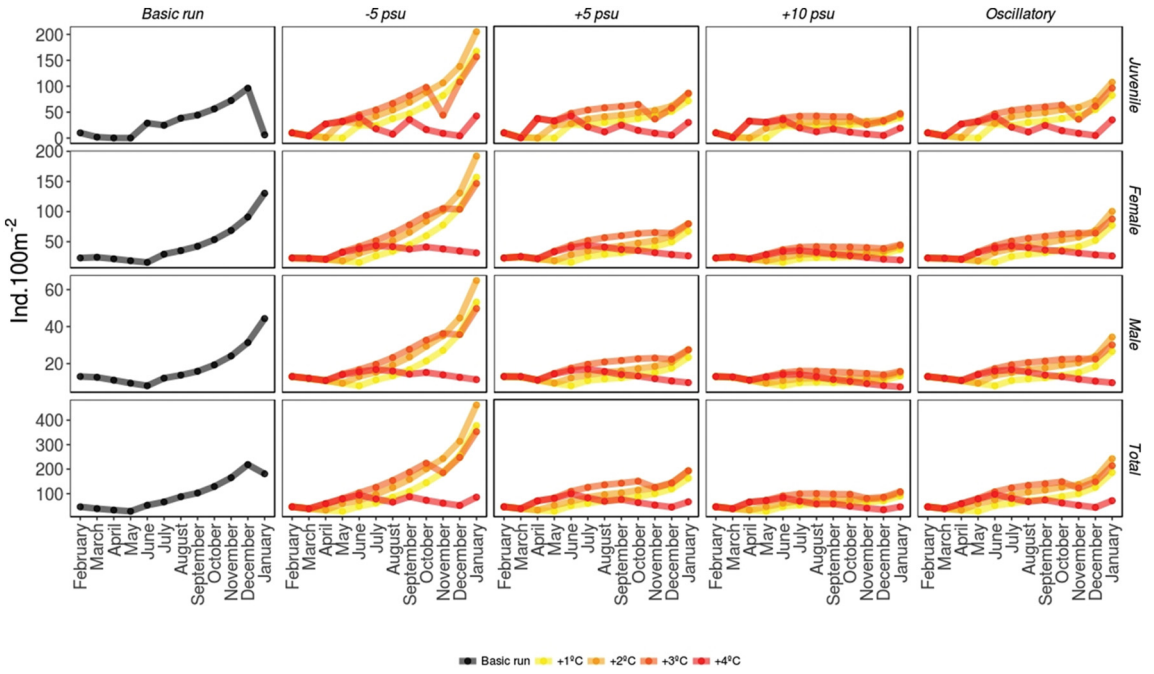

Fig. 7. One year simulations of juveniles, females, males and the total density (ind·100 m^{-2}) of the common goby *Pomatoschistus microps* in different scenarios of temperature and salinity changes. Oscillatory = −5 psu from November to April, and +5 psu from May to October.

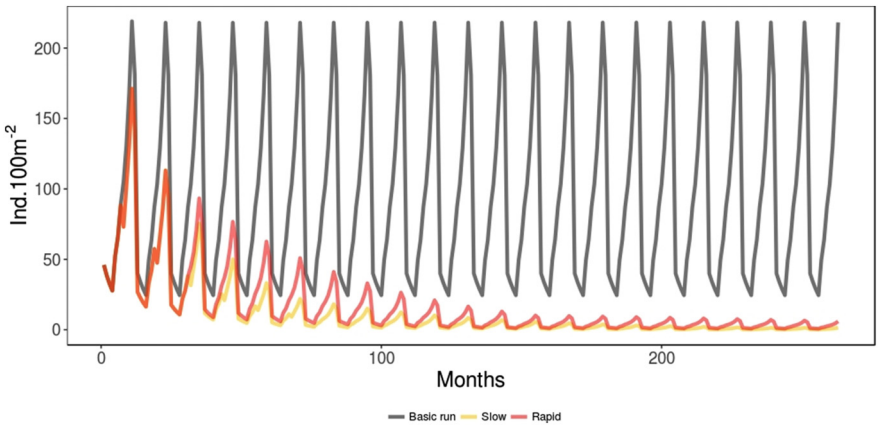

Fig. 8. Projection simulations of temperature increasing on *Pomatoschistus microps* population in Minho estuary, NW Iberian Peninsula. IPCC Slow scenario = +0.01 °C·y^{-1} and IPPC Rapid scenario = +0.04 °C·y^{-1}.

determine the optimal temperature for the growth of *P. microps*, all other values are assumed and may need to be reviewed in future studies.

The common goby population also responds negatively to salinity increases, indicating that droughts may cause a shrinkage in *P. microps* populations, which are in line with the results reported by Dolbeth et al. (2010), who observed a decrease in *P. microps* secondary production after drought events in the same studied site. On the other hand, model outputs suggested that *P. microps* population would be largely benefited by flood events, due to the decrease in salinity within the estuary. This agrees with Pampoulie et al. (2000), who described an increased reproductive investment by *P. microps* after a high freshwater inflow in a coastal lagoon in France. Also, the common goby seemed to be further benefited by the reduction of competitors such as, the sand goby *P. minutus*, within the lagoon (Pampoulie et al., 2000). Similarly, in a long-term study of *P. microps* population dynamics Nyitrai et al. (2013) showed that the species peaks in years with higher precipitation, which further reinforces that the species is benefited in scenarios of salinity decrease. Notwithstanding, the model showed that the effect of a reduced salinity in winter is voided when accompanied by an increase in salinity during summer, suggesting that *P. microps* populations would decrease in the next years, if the IPCC predictions of wetter winters and drier summers are accurate.

However, it is important to consider that the subsequent effects of climatic extremes may have opposite trends and negative feedback processes (IPCC, 2014). For instance, a massive die-off of bivalves after droughts (Ilarri et al., 2011) and floods (Sousa et al., 2012), may lead to a significant increase on the quantity of empty shells in the river bottom that might be used for *P. microps* reproduction in the next breeding season, which may led to an increase in the population density after one or more generations due to the persistence of these shells in the system for years (Ilarri et al., 2015b). Actually, the reproduction of common gobies seems to be limited by the presence of nest substrates (Nyman, 1953; Magnhagen, 1998) and their abundance and availability can directly influence the number of breeding males (Breitburg, 1987; Lindström, 1988).

The model was able to predict more accurately the dynamics of juveniles and females, while the predicted male dynamics differed more from real data, which may be related to the nest guarding behavior of males, that makes them difficult to be caught within estuaries (Miller, 1984) and, is considered as one of the reasons behind the apparent dominance of females in estuarine populations of *Pomatoschistus* spp. (Bouchereau et al., 1993; Fouda et al., 1993; Koutrakis and Tskliras, 2009). In fact, most of the dissimilarities between the observed and the predicted variation of male density occurred during the breeding season, which supports the idea that male guarding behavior may have influenced the results and lead to such dissimilarities, that are partially because this behavior is not accounted by the present model.

The model was most sensitive to variations in the reproduction parameters. This was somehow expected given that the common gobies present high plasticity on their reproductive traits (Reynolds and Jones, 1999; Pampoulie et al., 2000; Heubel et al., 2008), and suggests that the species can rapidly respond to environmental constrains and rapidly adapt to new environmental conditions. The uncertainty analysis showed that the model output is somewhat sensitive to uncertainty in the measurements of the data used to perform the model calibration

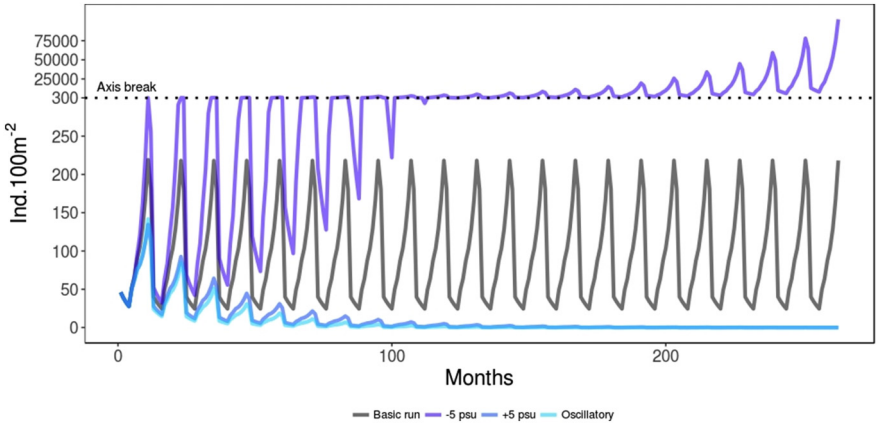

Fig. 9. Projection simulations of salinity variation on *Pomatoschistus microps* population in Minho estuary, NW Iberian Peninsula. Oscillatory = −5 psu from November to April, and +5 psu from May to October.

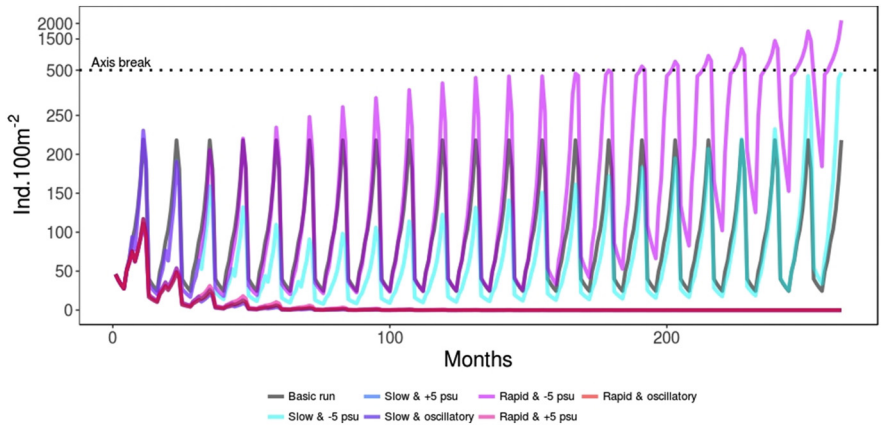

Fig. 10. Projection simulations of temperature increase combined with salinity variation on *Pomatoschistus microps* population in Minho estuary, NW Iberian Peninsula. Oscillatory = −5 psu from November to April, and +5 psu from May to October. Slow scenario = +0.01 °C·y^{-1} and Rapid scenario = +0.04 °C·y^{-1}.

(RRMSE = 17.82%). However the range of RRMSE obtained by recalibrating the model with the virtual data series was very narrow, with the RRMSE of the empirical model being well within that range, and thus can be considered to be accurate (Confalonieri et al., 2016).

Despite of the IPCC predictions referring to temperature increase in the air, it should be expected that the water temperature will also increase due to global changes in climate (Bates et al., 2008). Nevertheless, it is unlikely that water temperature will increase at the same rate of the atmospheric temperature, given the differences in the thermal properties between the two fluids; and hence, temperature increase in water probably would be smaller than in air. There are uncertainties in projected changes in hydrological systems since it often depends on a number of variables such as precipitation, evapotranspiration, soil moisture and runoff (Bates et al., 2008). In this context, we opted to use the IPCC projections for air temperature increase despite knowing that the temperature increase in water would be smaller. Nonetheless, it is unlikely that the water temperature would increase as much as the most extreme IPCC scenarios, therefore, the projections on the *P. microps* population dynamics at +3 °C and +4 °C should be seen with caution and understood as predictions for extreme climatic scenarios.

The model predicted that for every tested scenario of temperature increase, the *P. microps* population would experience a gradual decrease in projection simulations. Also, the most likely scenario of salinity change (oscillatory pattern) in extreme climatic events would lead to a sharp decrease in *P. microps* density. In this context, it is probable that during the next decades at Minho estuary, common gobies may experience population shrinkage. Given the trophic position and abundance of the species, this could cascade through the estuarine biological community, especially in a system where the species is remarkably abundant such as in Minho estuary (Souza et al., 2014). As a mesopredator, the common goby connects low and high levels of the food-web of fishes (Doornbos, 1984; Moreira et al., 1992; Cabral, 2000); therefore, changes in *P. microps* population would affect both higher and lower trophic levels, with its trophic role being even more relevant in systems where it achieves higher densities (Pockberger et al., 2014). Nevertheless, the real ecological impact of the *P. microps* population reduction is hard to predict, since the sympatric species *P. minutus* may play a similar ecological role (Salgado et al., 2004) providing a functional redundancy (Ives, 1995) and creating an "insurance effect" in the system (Yachi and Loreau, 1999; Loreau et al., 2003). Actually, both species are morphologically and ecologically similar, differing mostly on salinity preferences, with *P. minutus* preferring to inhabit saltier waters compared to *P. microps* (Leitão et al., 2006; Dolbeth et al., 2007). Also, both species can often compete for food and space (Złoch and Sapota, 2010) and hence, it is reasonable to assume that *P. minutus* may perhaps be benefited by a decrease in *P. microps* population, and potentially fulfill the ecological gaps left by the common goby. Notwithstanding, given the uncertainty about the ecological effects that a decrease in *P. microps* density might trigger, it would be interesting to perform further studies on the interactions between *P. microps* and *P. minutus* particularly at different conditions of temperature, salinity and density.

Given that the *P. microps* geographical range of occurrence is wide, and our study was conducted in a system located nearer to the southern edge of the species distribution (Froese and Pauly, 2016), the populations inhabiting systems at higher latitudes and thus subjected to colder temperatures could experience milder effects of climate change, while populations located further south may suffer more serious consequences. Still, given the plasticity of *P. microps*, each population may respond differently to environmental changes, and hence, each system should be treated as a unique case of study, despite the trend presented in this study, which predicts a decrease in *P. microps* density caused by warming waters.

The use of ecological models has been increasing in the last decades, with significant developments in the software tools available and also in their accuracy. Nonetheless, modeling approach still have limitations, which also include the IPCC projections themselves (Hollowed et al., 2013; Cheung et al., 2016). Population dynamics models are widely used but they require a good data set containing homogeneously distributed data. Additionally, the calibration of parameters in population dynamics models are especially difficult (Chatzinikolaou, 2012). The model we developed was tested against a dataset of 12 data entries, which is not a long time-series for this type of model, but is reasonable enough considering the life cycle of the species, the logistic constrains related to the sampling and the time-frame of the project. In addition, the model showed not to be affected by the uncertainty of the state variables and therefore was accurate in its outputs (i.e. low values of RRMSE = relatively high accuracy = model with relatively low susceptibility to uncertainty). Furthermore, it is also important to state that several parameters inputted into the model were obtained from different species and/or localities due to the lack of information in the literature about the common goby and the Minho estuary. These probably influenced the outputs of model, and for this reason, the outcome of our model needs to be seen with caution. Despite of these issues, the robustness of model and its design allowed us to drawn good and cautious interpretations regarding the direction and the magnitude of the shifts in the population dynamics of *P. microps*.

Our study did not account for limiting factors in the environmental carrying capacity to sustain a population increase of *P. microps*, therefore the model outputs ought to be seen with caution in this respect, and the magnitude of the population increase might not be realistic enough. For that reason it is important to take into consideration mostly the direction of the changes and the differences in strength among

scenarios. Nevertheless, our results point out to possible fate of *P. microps* population, and stakeholders can use this information to anticipate the consequences for the ecosystem. For instance, a decrease on the common goby population might have detrimental consequences for the fishery yield, given that the high abundance of *P. microps* certainly provides resources for carnivorous fishes targeted by fishermen, but further studies are needed in order to better comprehend the inter-specific responses towards the decline of *P. microps* population and its consequences for fishery.

7. Conclusion

The model for *P. microps* population dynamics seems to be effective in simulating the performance of the common goby in the Minho estuary when submitted to changes in temperature and salinity conditions. The obtained simulations are relevant in the context of the global climate (IPCC, 2014) since they demonstrated that the populations of *P. microps* in scenarios of temperature and salinity increase responded with a population decrease. However, in scenarios of a decrease in salinity, the population will experience a substantial increase in terms of density.

The obtained results presents a projection approach on how a core species will cope with climatic change in the near future. This type of approach represents a useful tool for future planning and management of estuarine systems, once the results predict how *P. microps*, an important component of estuarine biological communities, will vary with the global effects of climate change.

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